AQUATIC ADAPTATION IN REPTILES—PRIMARY OR SECONDARY?

By

† Alfred Sherwood Romer

Museum of Comparative Zoology, Harvard University, Cambridge, Mass.

A fair number of modern reptiles, such as the crocodilians, most chelonians and a number of ophidians, are amphibious to aquatic in habits and, in the Mesozoic, aquatic reptiles were abundant—ichthyosaurs, plesiosaurs and mosasaurs being the most prominent forms. Are such forms secondarily aquatic, descended from purely terrestrial ancestors, or may certain of them have been derived from primitive reptiles which had never completely abandoned the aquatic habitat of their lower vertebrate ancestors? Since the most positive definitive characteristic of the Reptilia is their amniote mode of development that freed them from the water, and since, farther back, limbs capable of terrestrial locomotion were developed in even the oldest known amphibians of the late Devonian, it seems reasonable, at first sight, to believe that early tetrapods rapidly emerged from the water onto land, and that water-dwelling was a secondary condition.

This is not necessarily the case. Despite the development of limbs in early amphibians, few members of this class ever achieved a truly terrestrial mode of life. And although the evidence is none too clear, it seems far from certain that all aquatic reptiles have reverted from land to water.

THE AMPHIBIAN STAGE

Let us broadly review the early history of tetrapods. The oldest known amphibians—the late Devonian ichthyostegids (Jarvik 1955)—were crossopterygian descendants which, despite the retention of certain primitive features, had developed their paired fins into short but sturdy tetrapod limbs, enabling them to leave the water and travel overland. Offhand, one would assume that with the development of paired limbs the ancestral amphibians immediately took up a terrestrial existence. But further reflection brings one to conclude that nothing could be further from the truth. For what purpose would these early amphibians come forth on to the land? It has been suggested that they were taking refuge from enemies in the water; but that can hardly be the case, for the amphibians are an offshoot of the rhipidistian crossopterygians who were the most predaceous of fishes in Devonian fresh waters. More reasonable, at first sight, is the belief that these fish descendants were setting forth to explore the terrestrial environment where new opportunities might await them. Here, however, the fatal objection is that there was precious little on land for them to eat. The rhipidistians were predaceous, eaters of smaller fishes and, presumably, freshwater invertebrates. It seems certain that all early amphibians

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were likewise eaters of animal food; universally, the teeth, like those of crosso-pterygians, were sharp-pointed conical structures quite incapable of dealing with vegetable materials. It is possible that there were already present on land in the Devonian some soft-bodied invertebrates which have escaped detection as fossils, but the only land animals known in the Devonian upon which a hope-fully terrestrial amphibian could feed were tiny Collembola (known from the Rhynie chert of Scotland) and a few myriapods. Most notably, not a single true insect is known from the Devonian.[1]

Amphibians attempting to live on land in the Devonian might admire the scenery; but they would surely starve to death. And in the early Carboni-ferous the terrestrial food supply was little better. One might expect primitive insects to appear, but none have as yet been found. It appears possible that in the Carboniferous scorpions were in process of migrating from water to land. But even the possible addition of scorpions to a diet of centipedes and micro-scopic soil-dwelling springtails does not appear to make life on land too attrac-tive for eaters of animal food. It was not until the later Carboniferous that land life really became possible with the appearance of a wealth of insects of primitive types. It is only toward the end of the Carboniferous that we find among early reptiles (and perhaps in one family of amphibians) forms which at long last were adapted to feed upon the readily available vegetation.

Why, then, the development of land limbs in amphibians? The answer, apparently, is a paradoxical one—that these limbs, which enabled them to walk on land, were an adaptation for water-dwelling under the conditions in which early amphibian evolution took place. Barrell (1916) long ago pointed out that the late Paleozoic, when tetrapod evolution was taking place, is charac-terized by an abundance of 'redbeds' formations. Beds of this sort are frequently indicative of their having been laid down under climatic conditions of seasonal drought such as are found in limited regions of the tropics today. For part of the year, rainfall is abundant, and life for water-dwellers is easy. When a drought comes, streams dry up, waters become stagnant, and oxygen is at a premium. However, a good fraction of Paleozoic freshwater fishes appear to have had lungs (which very few fish have today), and atmospheric oxygen was available to them if they came to the surface. But if the stream or pond dried up completely in the drought, what then? An ordinary fish would be, literally, stuck in the mud, and if the water did not return quickly would soon perish. But if rudimentary limbs of tetrapod type were present, the animal might be able to leave his dried-up pool, crawl up or down the streambed or even travel some distance overland, find a pool with water still in it, plunge in, and resume his normal aquatic life. Under seasonal drought conditions, tetrapod limbs, even if little developed, would be of immediate selective advantage to a freshwater dweller.

Watson years ago (1926) suggested this use of legs in the Carboniferous

[1] Originally described as insects were two specimens from the Devonian of the USSR; these, however, were subsequently recognized as crustacean.

and I have since pointed out (Romer 1957, 1958, etc.) that this situation may have been true of early amphibians generally. Had early limb development been for the 'purpose' of exploring land life, one would expect that the post-Devonian history of early amphibians would have exhibited the retention and even improvement of the limb development seen in the Devonian ichthyostegids. But the opposite is almost always the case. In the Carboniferous, with the frequent development of coal-swamp conditions, the importance of limbs as a means of survival under drought conditions would decrease; and if, in any standard text (such as Romer 1966: 87–98), we follow through the history of amphibians in the post-Devonian periods, we see, in accordance, a strong trend for limb reduction, rather than limb improvement, in most amphibian groups.

Pre-Jurassic amphibians are currently customarily divided into two major groups: the Lepospondyli (very probably an artificial assemblage) and the Labyrinthodontia. The Lepospondyli include a considerable variety of small Carboniferous and early Permian forms, apparently mainly coal-swamp dwellers, in nearly all of which the paired limbs are greatly reduced and may be lost completely. Exceptional are a number of late Carboniferous and early Permian members of the Microsauria in which rather well-developed limbs are present.

The much more important ancient group is that of the Labyrinthodontia. Here, as in the lepospondyls, there is in general a strong trend toward limb reduction, although not as marked or as rapid as was the case in most lepospondyls. We are not sure that the primitive ichthyostegids were directly ancestral to any later labyrinthodonts; however, one restricted series of Carboniferous forms, the Colosteidae (which I hope to discuss in the near future) may be ichthyostegid descendants; however, they have limbs more feebly developed than in the Devonian forms.

Ichthyostegids apart, however, nearly all labyrinthodonts may be arrayed in two main series, the Temnospondyli, in which a key character is the dominance in the vertebral column of the intercentrum, and the Anthracosauria, in which the pleurocentrum develops (to become eventually the true centrum of reptiles). The temnospondyls are by far the more abundant of the two, and are the only amphibians (apart from a 'pre-frog') present in the later Permian and Triassic. In some Carboniferous and early Permian forms the legs are reasonably well developed, as in the familiar *Eryops* of the early Permian which could quite surely waddle comfortably about its native swamps, and in one group, the dissorophoids, there was apparently, in the Permian, a considerable trend toward true terrestrial existence.[2]

But while limbs were maintained in proper fashion in certain temnospondyls, the trend toward reduction was strong within the group. Even among

[2] See, for example, the dissorophids *Cacops* and *Broiliellus* (Williston 1914, etc.), in which there were not only well-developed limbs but also dorsal armor, suggesting a terrestrial life where there was danger from reptile predators. These forms lived at a time in the Permian when terrestrial food was becoming more abundant.

primitive temnospondyls, such as the trimerorhachids, the limbs were much reduced, and from the later Permian on through the Triassic there was continued reduction, so that in typical Triassic members of the group, such as *Capitosaurus* and *Metoposaurus*, we find amphibians with a broad flat head and body with tiny limbs quite incompetent to support them out of the water. In the later Paleozoic and Triassic the dangers of seasonal drought were much less than in earlier days, and in correlation with this, there was a strong trend to reduction of the limbs. But if drought did occur, these late temnospondyls were helpless. I have described a locality in the Triassic of New Mexico (Romer 1939) in which a mass death of a myriad of metoposaurs ('*Buettneria*') occurred, obviously because of the drying up of the swamps and pools in which they lived.

The other main division of the labyrinthodonts is that of the Anthracosauria,[3] much less abundant but of interest as the group from which the Reptilia arose. Here, as in the temnospondyls, we see considerable variation in limb development. Most prominent of anthracosaurs in the Carboniferous (and persisting into the early Permian) were the Embolomeri, good-sized amphibians, essentially water-dwellers, quite surely with paired limbs of relatively small size which, nevertheless, could enable them to walk on land to some degree. Quite rare, known only from a few genera, were Carboniferous forms in which sturdy limbs persisted. One is *Gephyrostegus*, known only from two specimens from the European Upper Carboniferous; long confused with other genera, its nature and structure has been recently clarified by Carroll (1970*b*: 268–286). An apparently similar form, *Mauchchunkia*, has now been discovered in the Lower Carboniferous of Greer, West Virginia. So far there has been published (Hotton 1970) only an account of a fragmentary skull and incomplete skeletal materials. Now available to me, however, are two excellent postcranial skeletons, which I hope to describe shortly. The structure is quite similar to that of *Gephyrostegus*; we appear to have here a fortunate persistence of anthracosaurs with well-developed limbs through the 'hard times' (for potential terrestrial life) of the early Carboniferous. From forms of this sort the earliest reptiles presumably arose in the latter half of the Carboniferous. But also there may have come from this stock the Seymouriamorpha of the Permian, best known from *Seymouria* of the early Permian of Texas, but also represented by a number of European genera. Derived from the same general stock as the ancestral reptiles, the seymouriamorphs show many reptile-like characteristics, but although taking advantage of the relatively favourable conditions of Permian

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[3] O. Kuhn, in his *Handbuch der Palaeoherpetologie* (Panchen 1970), has, regrettably, tended to bring about confusion in amphibian terminology by substituting for Anthracosauria the Efremov term Batrachosauria (Efremov 1946) and reducing Anthracosauria to cover merely the embolomeres. But Efremov intended Batrachosauria (as the name implies) to apply only to reptile-like amphibians, notably the Seymouriamorpha, and not to such unreptile-like forms as the embolomeres. And for the latter Cope nearly a century ago coined the term Embolomeri, of which Anthracosauria, as used by Kuhn, becomes merely a junior synonym. I trust that Kuhn's nomenclatorial aberration here will be generally neglected and presently forgotten.

times to become essentially terrestrial in habits, they remained, it appears, in an amphibious stage as regards reproduction.

Above, we have reviewed the history of the older amphibious groups as regards their locomotor potentialities and general mode of life. Tetrapod limbs were early developed and in a few cases, such as Permian dissorophoids and seymouriamorphs, were not merely retained but used for terrestrial locomotion. But in general there appears to have been a strong trend for limb reduction. The story agrees well with the assumption that the Amphibia were, and generally remained, aquatic or at the most amphibious in habits; that limb development at the beginning was not related to any trend toward terrestrial life but as a useful aid to successful aquatic life under seasonal drought conditions; and that when such climatic conditions were lessened, limb reduction very generally took place.

EARLY REPTILES

What was the mode of life of the earliest reptiles, descended from water-dwelling amphibian ancestors? How rapidly did they take on the terrestrial mode of life, facilitated by the 'invention' of the amniote type of development? In recent years it has become increasingly clear that the basic stock of the Reptilia lies in the cotylosaur group termed the Captorhinomorpha. Members of this group have long been known from the early Permian, but in recent years it has become clear, mainly through an excellent series of papers by Carroll (1969, 1970b, etc.), that they were already flourishing in the late Carboniferous (the Pennsylvanian of American usage). We are here at a stage when, in contrast to earlier times, true land life had at long last become possible; with a known wealth of primitive insects present, there was now available a basic source of food upon which a terrestrial fauna might feed. Central in this picture are members of the family Romeriidae. These were small reptiles whose appearance in life might have been rather like that of modern lizards, but which were very different from any modern reptiles in that their structure was of a very generalized and primitive type, of a sort from which, one may believe, later reptiles of almost any group might have been derived. Still more primitive are members of the family Limnoscelidae. The type form, *Limnoscelis palustris* (Williston 1912; Romer 1946), is of early Permian age, but representatives are now known from the Carboniferous, and one form, *Romeriscus* (Baird & Carroll 1967) from the Westphalian A of Cape Breton, is the oldest known reptile. It seems certain (as the scientific name suggests) that the limnoscelids were persistently primitive in retaining amphibious habits. But it is generally agreed that the limnoscelids were already technically reptiles, strongly suggesting that the amniote type of development had already been invented before the reptiles had abandoned the amphibious mode of life of the older tetrapods.

Carroll believes, however, that the limnoscelids were too archaic in structure to have been a group from which the radiation of later reptilian groups

could have taken place, and that the basic stock from which higher reptiles evolved was that of the more advanced family Romeriidae. What was the mode of life pursued by the romeriids—was it, at this level, completely terrestrial, or were these forms still somewhat aquatic in habits? Carroll gives a good argument for the terrestrial side of the question—namely, that the skeleton in romeriids is well ossified, whereas in amphibious reptiles, generally, ossification is less complete. Had we good continental beds in the Upper Carboniferous, with a true land fauna, the case for the purely terrestrial nature of the romeriids would be greatly strengthened. Unfortunately, our knowledge of Upper Carboniferous vertebrate faunas is almost entirely confined to those of coal swamps. In these, as at Linton and Mazon Creek, romeriids are relatively rare, but are present. Only in the fossil tree stumps of the Nova Scotia Joggins does Carroll (1969: 36) believe that he has a truly 'terrestrial' fauna in which romeriids are abundant.

I have a very high regard for Carroll's work on Carboniferous tetrapods, but I think that here he has (like the contained fauna) fallen into a trap. The Joggins region, well known since the days of Dawson (and recently redescribed briefly by Carroll and others in 1972) consists of a series of Carboniferous exposures along the bluffs at the head of the Bay of Fundy in western Nova Scotia. Here there are present thousands of feet of Upper Carboniferous deposits which include some dozens of coal seams separated by intervening shales. We are dealing with a long-persisting coal basin in which, time after time, a coal swamp developed. Between successive swamp deposits the area was invaded by mud flows which hardened into shales. The lycopod trees of the coal swamps tended to die, leaving hollow stumps that (as well shown by Carroll 1970a, fig. 3) acted as traps for unwary amphibians and reptiles which wandered about the mud flats of the region in the periods between times of coal seam formation. The contents of the traps consist mainly of romeriids, microsaurs with well-developed limbs, and a rhachitome (*Dendrerpeton*) with rather good legs; absent are nectrideans, aïstopods and other coal-swamp dwellers in which limbs were lost or poorly developed. Is this a 'terrestrial' fauna? Hardly. We are still present in a coal-swamp basin, and there is no guarantee that we are not within a short distance of the water. It simply means that we have a selective screening of a coal-swamp fauna. As Rayner (1971) notes: 'The pure water-dwellers, such as the aïstopod and nectridean lepospondyls, are absent. Those found are more 'terrestrial' than in other Carboniferous faunas; they walked, ambled or waddled across the muddy or sandy flats among the rotting tree trunks. The sediments they traversed, however, and which finally buried animals and trees, were purely aqueous—the normal type laid down in the open stretches of the coal forests and swamps.'

It is highly probable that some Carboniferous romeriids were completely terrestrial; but those which we do know were persistent coal-swamp dwellers. It would appear, as far as present knowledge goes, that despite the advantage given them by their amniote mode of life, and despite the fact that the abundant

insect fauna of the later Carboniferous afforded a terrestrial food supply for eaters of animal food, early reptiles were slow to abandon the amphibious mode of life of their ancestors.

By the close of the Carboniferous and the beginning of the Permian, many reptiles were already fully 'ashore' and even (as shown for example by the presence of *Edaphosaurus* in the late Carboniferous) some were shifting from animal to vegetable food supplies. As noted later, in the case of many aquatic and amphibious reptiles of the Mesozoic and Cenozoic, evidence is lacking as to whether or not the forms leading to them had become fully terrestrial and only later returned to the water. Is there, however, any evidence in early reptile history suggesting a primitive retention of an amphibious to aquatic habit? Apart from the primitive limnoscelids, there are two positive examples of water-dwelling reptiles which are of such an early age that it seems unlikely that their pedigree included forms which had become completely terrestrial in habits.

One example is *Mesosaurus* of South Africa and southern Brazil (Rayner 1971: 472–476). The phylogenetic position of this small amphibious reptile is uncertain (it has been variously referred to the diapsids and synapsids, and some recent evidence suggests that it may be anapsid—an early cotylosaur offshoot). Highly specialized for feeding on minute crustaceans, *Mesosaurus* occurs at a horizon close to the Carboniferous-Permian boundary in the 'white band' of the South African Dwyka and comparable beds in Brazil. Occurring at this early stage in reptilian history, it is difficult to believe that its ancestors could have become completely terrestrial and then rapidly shifted back to an amphibious mode of life, with the speedy acquisition of its unique type of cranial and dental structures.

More striking is the story of the ophiacodont pelycosaurs. The subclass Synapsida, of which the pelycosaurs are the primitive members, is in its more advanced stages an almost purely terrestrial group. But while among the pelycosaurs the sphenacodontoid and edaphosauroid suborders are terrestrial in nature, *Ophiacodon* and its relatives, most primitive of pelycosaurs, are quite surely still amphibious in habits (Romer & Price 1940). The two other pelycosaur groups flourished greatly in the early Permian, but only appear in the fossil record at the very close of the Carboniferous. Quite different is the story of the ophiacodonts. One ophiacodont, *Clepsydrops*, has long been known from the Upper Carboniferous of Danville, Illinois, and it has been demonstrated that ophiacodonts were present nearly as far down in the sequence of Carboniferous coal-swamp deposits (Romer 1961; Carroll 1964; Reisz 1972) as reptiles of any sort.

The ophiacodonts differ little from primitive captorhinomorphs, apart from the development of the synapsid temporal opening, and it seems completely reasonable to believe that this basal group of synapsids branched off from the basal reptile stock while this was still persistently amphibious in habitat.

LATER AMPHIBIOUS AND AQUATIC REPTILES

Notable in the known paleontological history of reptiles is our almost complete lack of knowledge of groups other than cotylosaurs and synapsids until late Permian and Triassic days, and the early stages in the evolutionary story of most reptile groups is purely guesswork. For example, the Chelonia is an order which includes among the tortoises a few purely terrestrial forms, and on the other hand gave rise to a number of high seas types, but in general they are typically amphibious in habits.

The first chelonians appear in the late Triassic, and while a bit more primitive in some regards, already show the basic structural pattern of the order and, it would seem, lived the typical amphibious life characteristic of most of their descendants. It is quite possible that in the long stretch of time between the Carboniferous and the late Triassic the chelonians had become purely terrestrial and then reverted to an aquatic mode of life. But it is equally possible that we have in the typical members of this order a retention of a truly primitive mode of amphibious life.

Unknown, too, is the pedigree of the great group of aquatic reptiles currently grouped in the subclass Euryapsida—the placodonts, nothosaurs and plesiosaurs. The mollusc-eating placodonts and the nothosaurs appear in the Middle Triassic oceans; in the Jurassic these forms disappear, to be replaced by the purely aquatic plesiosaurs, which had a spectacularly successful career in the middle and later parts of the Mesozoic. Where did these euryapsids come from? We have no clues as to their history. *Araeoscelis* of the early Permian has an euryapsid type of temporal opening, but Vaughn (1955) has pointed out that this genus shows no resemblance to later euryapsids in other regards.

Similarly blank is the history of the ichthyosaurs, most completely adapted of all reptiles to a marine existence. The ichthyosaurs first appear in the Middle Triassic, and although the members of the order were at that time somewhat less advanced than their abundant Jurassic (and less abundant Cretaceous) descendants, they were already definitely ichthyosaurs, quite distinct from members of any other reptilian group. I have recently (Romer 1968) demonstrated that, in contrast to earlier beliefs, their temporal structure was similar to that of the typical euryapsids; but this only adds further puzzlement to the problem of their ancestry. I have pointed out (Romer 1948) that except for the temporal opening, their skull structure is basically similar to that of ophiacodont pelycosaurs, and like these pelycosaurs, could reasonably have originated from captorhinomorph cotylosaurs. But there is absolutely no trace of transitional forms. The ichthyosaurs could, like the ophiacodonts, have come directly from early reptiles still in an amphibious ecological condition. But the gap in time between the Carboniferous and Middle Triassic is great enough so that it is possible to argue here, as in the case of euryapsids and chelonians, that their ancestors might have become purely terrestrial and secondarily reverted to aquatic life.

The archosaurs, which include, as well as ancestral thecodonts and croco-

dilians, the great dinosaurian orders, the flying pterosaurs and bird ancestors, appear at first sight to have been *ab initio* a terrestrial group, in which there was a strong tendency toward a bipedal stance and, in pterosaurs and birds, on toward aerial life. But Charig (1966) has recently pointed out that there are suggestions of amphibious habits in early archosaurs. The strong hind legs and tail which were highly useful in the development of bipedal habits, may have been initially developed in relation to an amphibious mode of life (*Mesosaurus* is comparable). Further, many early archosaurs show aquatic tendencies (Charig & Reig 1970). The oldest and most primitive of archosaurs, the Proterosuchidae (such as '*Chasmatosaurus*') were quite certainly amphibious in habits; crocodilians developed early from the thecodont base; the most abundant of later Triassic thecodonts were the amphibious crocodile-like phytosaurs; and the Middle Triassic thecodonts include a further family, Proterochampsidae, which were certainly phytosaur-like in habits (Romer 1971). All in all, it is not impossible that the ancestral archosaurs were derived from primitive reptiles which were still amphibious in habits. But the first known archosaur is late Permian in age, and it can be argued, as in the groups already discussed, that their ancestors had become completely terrestrial in Permian times before amphibious trends developed.

Of all reptile groups it is the Lepidosauria—the lizards, snakes, and rhynchocephalians—for which the best argument for a firm terrestrial ancestry can be made. The ancestors of the subclass, the Eosuchia, appear before the end of the Permian, and there is no positive evidence of any aquatic trend in the group. There are, to be sure, sea snakes and some water-living lizards in the recent fauna, but derivation of them from terrestrial ancestors can be reasonably made. *Champsosaurus* of the late Cretaceous and earliest Tertiary is amphibious, and certain Jurassic forms look suspiciously amphibious in nature but descent from terrestrial ancestors can be reasonably argued. Most prominent of aquatic lepidosaurs were the mosasaurs, which flourished greatly in the late Cretaceous; but these can be derived from amphibious ancestors in the early Cretaceous and, hence, mosasaur descent from Jurassic terrestrial forms can be reasonably argued.

If we attempt to sum up this story of terrestrial versus aquatic trends in reptile history, it seems that the Reptilia were not too speedy in the late Paleozoic in leaving their ancestral home in fresh waters; and that some, at least, of the aquatic and amphibious members of the group may have persistently retained a primitive mode of life rather than having returned to the water from a purely terrestrial ancestry. But the question in many cases must remain an open one until new fossil evidence appears to fill in the major gaps still present in the Permian and early Triassic history of reptiles.

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